

TIME-ACTIVITY BUDGET OF WILSON'S AND SEMIPALMATED PLOVERS IN A TROPICAL ENVIRONMENT

ALAIN MORRIER AND RAYMOND McNEIL¹

ABSTRACT.—We compared seasonal variations in the daylight activity budget of Semipalmated (*Charadrius semipalmatus*) and Wilson's plovers (*C. wilsonia cinnamominus*) in northeastern Venezuela. The former are Nearctic migrants which use the area as a migratory stop-over and wintering area; the latter are residents and breed in the region. Feeding, resting, and aggressive manifestations are the three main activity categories. The seasonal activity patterns of the species differ. In both species, the seasonal pattern of time spent resting is the inverse of that for feeding. From October to April, Semipalmated Plovers fed during most of their daylight time in spite of a decrease in feeding in January and February. In contrast, Wilson's Plovers devoted more time to resting than to feeding from November to April (the non-breeding period). In both species, the seasonal variations in the time spent feeding during daylight can be explained by variations in their energetic needs, e.g., for molting and building fat reserves. Time devoted to aggression was very low in both species but increased in March–April for Wilson's Plovers, just before the beginning of reproductive activities. Daily energy expenditure and energy intake were estimated for Wilson's Plovers, supposing that they were resting from dusk to dawn. From November to March, daylight feeding alone was insufficient to counterbalance energy expenditure, indicating that they foraged primarily during nighttime. *Received 14 Jan. 1991, accepted 6 June 1991.*

Some migratory shorebirds continue accumulating fat reserves during the few weeks following their arrival in coastal habitats of northern South America before departing for regions farther south (McNeil 1970a). From about November to February, shorebirds lose weight before starting to deposit large fat reserves in March–April in preparation for their northward migration to the breeding grounds (McNeil 1970a). This occurs commonly in migratory species within the genera *Charadrius*, *Pluvialis*, *Tringa*, *Limnodromus*, and *Calidris* which breed in northernmost North America. However, some shorebirds (e.g., Wilson's Plover [*C. wilsonia*] and Black-necked Stilt [*Himantopus mexicanus*]) are sedentary and permanent residents in the Neotropical region, and share tropical environments together with species migrating from the Nearctic region (McNeil et al. 1990). These Neotropical residents, contrasted to migrants, have only small fat reserves which are made up immediately before the breeding season or just before a food-shortage period (McNeil 1970b, 1971).

Myers and McCaffery (1984) suggest that the frequency and duration of the food intake in migratory species should vary seasonally. For ex-

¹ Dépt. de Sciences biologiques, Univ. de Montréal, C. P. 6128, Succ. "A," Montréal, Québec Canada H3C 3J7.

ample, birds must eat when (1) refueling at a stop-over place after a long non-stop over-sea flight, (2) molting, or (3) accumulating fat in preparation for migration. In contrast, for allied or congeneric species residing the entire year in the Neotropical region, seasonal variations in the energy intake should be less. The food intake should be higher at the beginning of the breeding season than in the other periods. Little is known concerning the activity budget of shorebirds wintering or residing in tropical environments. The only available data from regions of high temperatures were provided by Puttick (1979) for the Curlew Sandpiper (*Calidris ferruginea*) in South Africa, Hockey (1984) for the African Black Oystercatcher (*Haematopus moquini*), and Maron and Myers (1985) for the Sanderling (*C. alba*) in California. In addition, Zwarts et al. (1990) have shown that the lowest feeding activity in nine of 14 Palearctic shorebird species wintering in Mauritania was observed in February and that the activity was at a maximum in March–April.

In this paper we compare the seasonal variations in the daylight activity budget of Semipalmated (*C. semipalmatus*) and Wilson's plovers in a tropical environment. The former breeds in North America and winters from southern United States to southern South America (Hayman et al. 1986). There are three subspecies of Wilson's Plovers: *C. w. wilsonia*, *C. w. beldingi*, and *C. w. cinnamominus* (Hayman et al. 1986). The race *cinnamominus* is a permanent resident of the Caribbean, the Atlantic coast of northern South America from Colombia to northeastern Brazil, and the islands off Venezuela in the Caribbean Sea. The Semipalmated Plover and the Wilson's Plover (*cinnamominus*) occur together on the coast of northern South America, in particular in the coastal lagoons of Venezuela (McNeil et al. 1990). The seasonal variations in the fat content of both species were documented by McNeil (1970a, b). After a preliminary analysis of the data on the daylight activity budget of Wilson's Plovers, we examined seasonal variations of its daily energy budget. The same approach was not possible for the Semipalmated Plover since it was almost impossible to collect data on the size and identity of its prey.

STUDY AREA AND METHODS

The study was done in the Chacopata lagoon complex (10°41'N, 63°46'W) on the north side of the Araya Peninsula, State of Sucre, in northeastern Venezuela. Up to 300 Semipalmated Plovers have been observed in August and September at Chacopata during fall migration (Limoges 1987). Their average number decreases to 100 individuals from the end of October to December and increases to about 250 birds between January and April. Spring migration occurs at the end of April and the beginning of May (Limoges 1987). The population of Wilson's Plovers is highest in August–September (around 100 birds) and decreases to about 10–20 birds in October due to post-breeding dispersal and regional movements.

The breeding population is about 50 individuals. Pair formation and the beginning of breeding activities occur in March–April (Limoges 1987).

Semipalmated and Wilson's plovers were observed from 18 October 1985 through 20 April 1986. All observations were made using a 20× spotting scope and 7 × 28 binoculars. Their activities were recorded using focal sampling procedures (Altmann 1974) during 15-sec intervals. Activities were grouped under six functional categories: (1) feeding—pecking at substrate, walking and running in pursuing prey, waiting or pausing while hunting prey, eating prey, drinking, and foot-tapping; (2) resting—motionless, huddled on the dry mud or on sand, sleeping with head tucked in plumage, often standing on one leg; (3) aggression—ground or aerial chases, fights, ground or aerial escape, ground displays, alert due to agonistic interactions; (4) preening—preening, bathing, and comfort movements; (5) locomotion—walking, running, and flying not associated with foraging, aggression, or being alert; (6) being alert—aerial escape of a predator or flying for an unknown reason, low crouching posture, and other alert movements (e.g., head-bobbing). Only one bird was observed at a time, and for as long as possible. When it was lost from sight, another one was selected. We were unable to collect data on the Wilson's Plover in the second half of December and February, and the first half of April, and on the Semipalmated Plover in the first half of January and April.

We tried to sample the duration of total daylight period every two weeks by observation periods of 1–12 h distributed over sampling sessions of 1–5 consecutive days (Tables 1 and 2). However, the plovers were sometimes momentarily out of sight. Consequently, as a measure of the relative importance of the time devoted to each activity category during the total daylight period, we calculated a daylight time-activity index (TAI) per session

$$TAI_i (\%) = \frac{TTA_i \times 100}{TDO} \quad (1)$$

where TTA_i = total time (min) spent in a given activity category (i) during the sampling session, and TDO = total duration of the observations (min) during the sampling session (Tables 1 and 2). Time-activity indices (TAI_i) of the two plovers were compared, for each activity category, with the Student *t*-test.

Equation (1) gives a single value of TAI_i per activity and per sampling session. With single values per sampling session, statistical analysis of the seasonal variation in the time devoted to a given activity is not feasible. Therefore, the duration of the daylight period of the middle day of each sampling session (each sampling session lasted between 1–5 consecutive days; Tables 1 and 2) was divided into 24 intervals of equal duration. In order to measure the relative importance of the time devoted to each activity category during each interval, we calculated a time-activity index per interval ($TAII$) as follows:

$$TAII_i (\%) = \frac{TTA_{iI} \times 100}{TDOI} \quad (2)$$

where TTA_{iI} = total time (min) spent in a given activity category (i) during the interval, and $TDOI$ = total duration of the observations (min) during the interval.

We used ANOVA to test the statistical significance of the variance of the $TAII_i$ values between the different daylight periods for each activity category. Daylight periods were then compared *a posteriori* with Duncan's multiple range test (Scherrer 1984). One exception was for the time-aggression indices (TAI_{agI}) of the Wilson's Plover which were divided *a priori* into two time periods: (1) from October to February and (2) the beginning of the breeding period (March–April). Both periods were compared by the use of the Student *t*-test.

TABLE 1

SAMPLING CALENDAR OF SEMIPALMATED PLOVERS GIVING, FOR EACH SESSION, THE DURATION OF THE DAYLIGHT PERIOD, THE TOTAL DURATION OF THE OBSERVATION, THE PERCENTAGE OF THE DAYLIGHT PERIOD COVERED BY OBSERVATIONS, AND THE TOTAL NUMBER OF BIRDS OBSERVED

Sampling sessions	Duration of the daylight period (h:min)	Total duration of observations during the sampling period (h:min)	Percentage of the daylight period covered by observations	Total number of birds observed
25–26 October	11:50	8:06	68.42	28
11–13 November	11:44	8:10	69.75	28
22–24 November	11:36	7:17	62.82	33
4–6 December	11:33	7:21	63.74	21
13–17 December	11:31	7:22	63.74	11
20–24 January	11:33	9:22	81.10	18
3–4 February	11:43	10:07	86.34	25
19–20 February	11:50	8:59	75.92	34
16–18 March	12:04	8:29	68.96	9
27–31 March	12:07	8:30	70.15	31
16–20 April	12:22	8:56	72.34	33

The daily energy expenditure (DEE; 24-h, including the night) for free-living Wilson's Plovers was estimated by summing the time spent in each activity, such as foraging and walking, times the caloric equivalent of each category, as follows (King 1974):

$$DEE = \sum(T_i K_i BMR) \quad (3)$$

where T_i = time spent (min) in the activity category i , K_i = increment factor, as multiple of the BMR, allocated to each activity category (i) (Table 3), and $BMR = 0.0808W^{0.734}$ (Aschoff and Pohl 1970), where BMR is the basal metabolic rate in kJ/h and W is the average body mass (g) of individuals captured monthly in the Chacopata lagoon. For each daylight period, the energy intake (EI) of Wilson's Plovers was calculated using the following formula (adapted from Puttick 1980):

$$EI = \sum[(T_f R_f n_i)(m_i e_i A)] \quad (4)$$

where T_f = total daylight time spent foraging (min), R_f = mean rate of foraging (mean number of prey taken/min), n_i = percent of i th prey item in diet, m_i = dry mass of organic matter of i th prey item (g), e_i = energy content of i th prey item (kJ/g of dry mass), and A = assimilation efficiency = 0.65 (as determined for *Uca tangeri* by Zwarts and Blomert [1990]).

Small fiddler crabs (*Uca thayeri*) comprised 98.6% of Wilson's Plover prey. The plovers were observed catching very small, unidentified, other prey types only on four other occasions. Size estimates of crabs were based on the carapace width of the crabs in comparison with plover bill lengths. Thus, prey items (i) differed only in size, not in species. Undamaged crabs of different sizes were collected and the maximum width of their carapace was measured to the nearest 0.1 mm. They were dried at 60°C for 8–12 h, and the dry mass (m_i) was determined to 0.001 g. Energy content (e_i) of different crab sizes was obtained with a Phillipson's microbomb calorimeter. Sulphide and nitrate contents were negligible and were

TABLE 2

SAMPLING CALENDAR OF WILSON’S PLOVERS GIVING, FOR EACH SESSION, THE DURATION OF THE DAYLIGHT PERIOD, THE TOTAL DURATION OF THE OBSERVATION, THE PERCENTAGE OF THE DAYLIGHT PERIOD COVERED BY OBSERVATIONS, AND THE TOTAL NUMBER OF BIRDS OBSERVED

Sampling sessions	Duration of the daylight period (h:min)	Total duration of observations during the sampling period (h:min)	Percentage of the daylight period covered by observations	Total number of birds observed
18–21 October	11:52	8:36	72.47	12
11–12 November	11:44	7:28	63.67	13
21–22 November	11:36	9:25	78.92	6
1 December	11:34	10:21	86.64	6
14–16 January	11:35	11:01	95.11	8
29–30 January	11:40	10:17	88.14	14
15–17 February	11:48	11:10	94.70	7
8–9 March	11:59	11:06	92.63	7
22–24 March	12:08	11:13	92.45	8
11–13 April	12:19	10:10	82.54	16

not taken into account in calculating the energy content. Results were expressed in terms of kJ/g of dry mass. A correction (i.e., 0.6 kJ/g of CaCO₃) was made for the endothermic reaction during the combustion caused by decomposition of CaCO₃. Based upon data of Zwarts and Blomert (1990) for *U. tangeri*, the CaCO₃ content of *U. thayeri* was estimated equal to 30% of their dry mass.

Wilson’s Plovers were mist-netted at monthly intervals and weighed to the nearest gram.

TABLE 3

VALUES FOR THE K-FACTORS ALLOCATED TO EACH ACTIVITY CATEGORY IN CALCULATING DAILY ENERGY EXPENDITURE OF WILSON’S PLOVERS

Activities	kJ/h	References
Foraging	2.0	Orians 1961
Resting	1.24	King 1974
Preening	1.8	Wooley and Owen 1978
Flight ^a	12.0	King 1974
Walking	1.7	Wooley and Owen 1978
Fight	15.2	Maxson and Oring 1980
Ground display	4.0	Maxson and Oring 1980
Alert ^b	3.4	Maxson and Oring 1980
Running ^c	2.0	Fedak et al. 1977
Nocturnal resting	1.25	King 1974

^a Including all flights associated with alert reactions, agonistic manifestations, and locomotion.
^b Including alert reactions associated with aggressiveness, but excluding flight escape.
^c Including running for feeding, or ground pursuit and escape.

RESULTS

Daytime activity budget.—Except in January and February, feeding was the principal activity of Semipalmated Plovers and accounted for an average of $60.0\% \pm 13.9$ of their time (Fig. 1). Percentage of time devoted to foraging varied significantly during the study period ($F = 7.61$, $P < 0.001$). October, December, and March–April were characterized by time-foraging indices ranging from 68.6–86.1%, while in November and January–February foraging ranged from 31.7–46.7% of the day. Significant differences in the fraction of daylight hours spent feeding took place between October and November, November and December, December and January, and finally between February and March. In contrast, time devoted to feeding by Wilson's Plovers averaged only $17.0\% \pm 12.5$, but showed significant seasonal variations ($F = 9.17$, $P < 0.0001$) with values for the time-foraging indices of 55.0 and 42.7% for the end of October and the beginning of April, respectively, and ranging from 1.2 to 15.4% from November to March (Fig. 1). Foraging was the principal activity of Wilson's Plovers only at the end of October.

Semipalmated Plovers, consistently and significantly, devoted more time to feeding than Wilson's Plovers ($t = 5.12$, $P < 0.0001$).

Wilson's Plovers rested significantly more during their daylight period (average = $77.8\% \pm 12.6$) than Semipalmated Plovers (average = $29.0\% \pm 13.5$; $t = 5.88$, $P < 0.001$). In both species, time spent resting showed significant seasonal variations ($F = 8.05$, $P < 0.0001$ for the Semipalmated Plovers; $F = 7.51$, $P < 0.0001$ for Wilson's Plovers) and followed a pattern strictly inverse of the time spent feeding (Fig. 2). Time devoted by Semipalmated Plovers to agonistic behavior was always extremely low (average = $0.1\% \pm 0.1$; Fig. 3), except at the end of October when their time-aggression index (0.7%) was significantly higher than in other periods ($F = 2.97$, $P < 0.01$). However, during three consecutive days at the beginning of October, one color-banded bird was observed regularly directing agonistic activity towards conspecific intruders while defending a feeding territory. During the same period, another individual defended an adjacent territory. The former was never seen in the lagoon thereafter; it was likely a bird in transit to other regions farther south. Interspecific interaction involving Semipalmated Plovers was noted only twice, in March, when two individuals forced a small peep sandpiper (*Calidris* sp.) out of their feeding area.

Aggression accounted, on average, for only $0.6\% \pm 0.4$ of the daylight time-budget of Wilson's Plovers (Fig. 3) but increased significantly in March–April (1.2 to 1.6%) in comparison with other months (0.02–0.5%; $t = 3.72$, $P < 0.01$). As for Semipalmated Plovers, agonistic manifestations

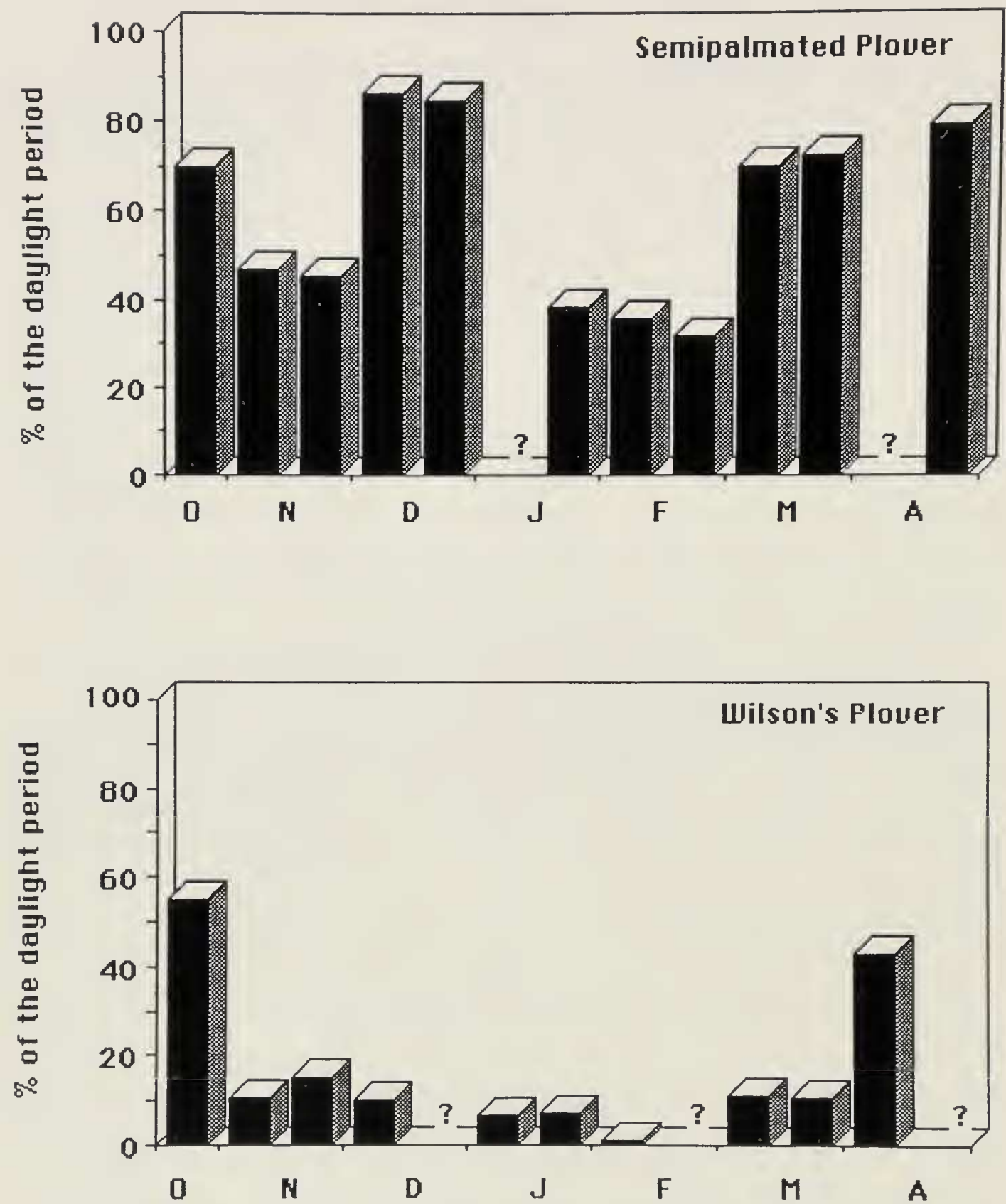


FIG. 1. Seasonal variations in the relative importance of time devoted to feeding during the daylight period. Interrogation marks (?) indicate the absence of data.

of Wilson's Plovers were strictly intraspecific except in two cases: in November, one individual chased a Semipalmated Plover from its resting area and at the beginning of March another one displaced a feeding Short-billed Dowitcher (*Limnodromus griseus*).

Wilson's Plovers devoted significantly more time to aggression than did Semipalmated Plovers ($t = 2.46, P < 0.05$) except at the end of October

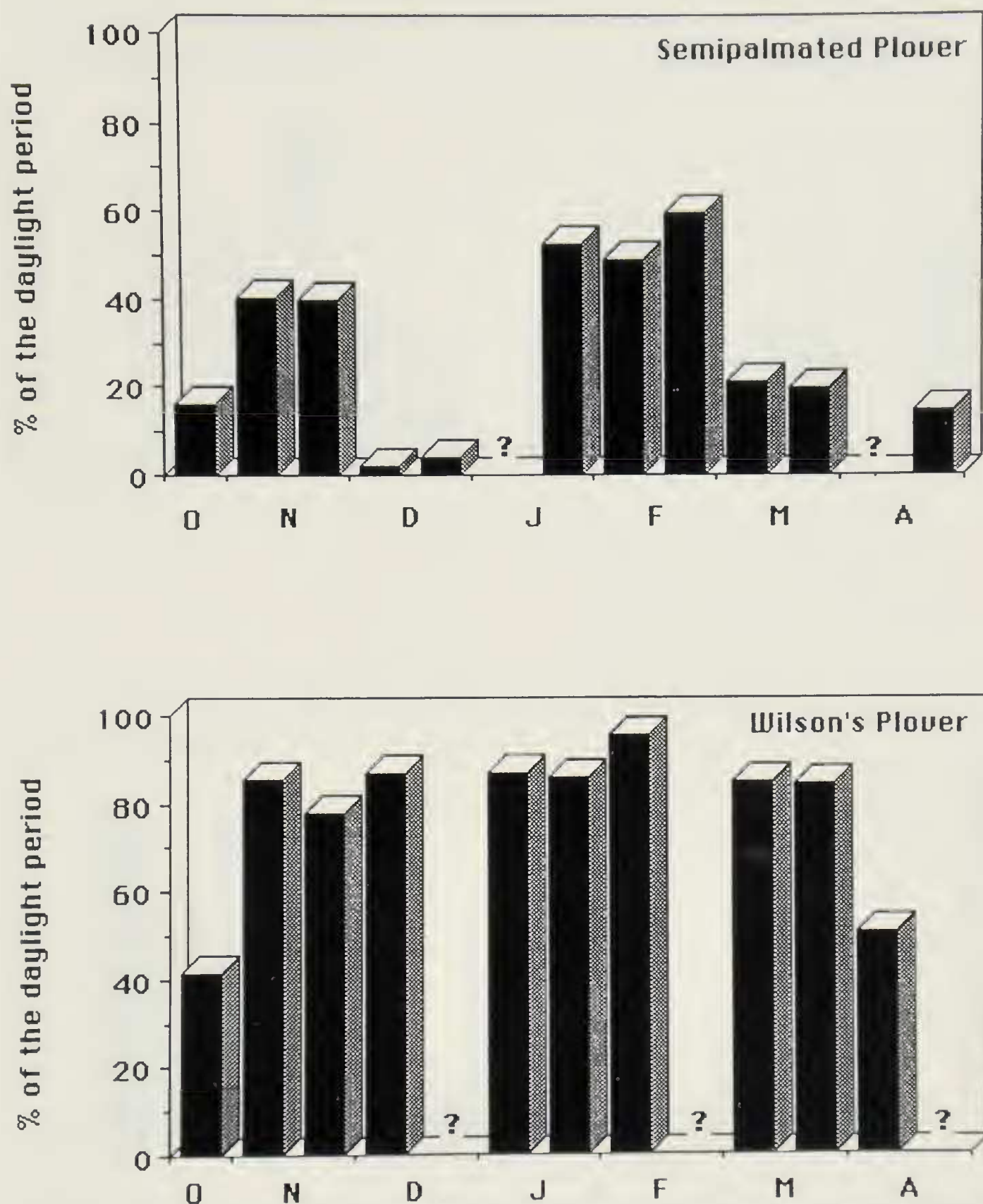


FIG. 2. Seasonal variations in the relative importance of time devoted to resting during the daylight period. Interrogation marks (?) indicate the absence of data.

(Fig. 3). In addition, the increase in aggressiveness in March–April in the former was not observed in the latter.

Semipalmated Plovers preened significantly more on the average ($4.9\% \pm 1.0$) than did Wilson's Plovers ($1.8\% \pm 0.5$; $t = 4.72$, $P = 0.001$). However, there were no significant seasonal variations in this activity category.

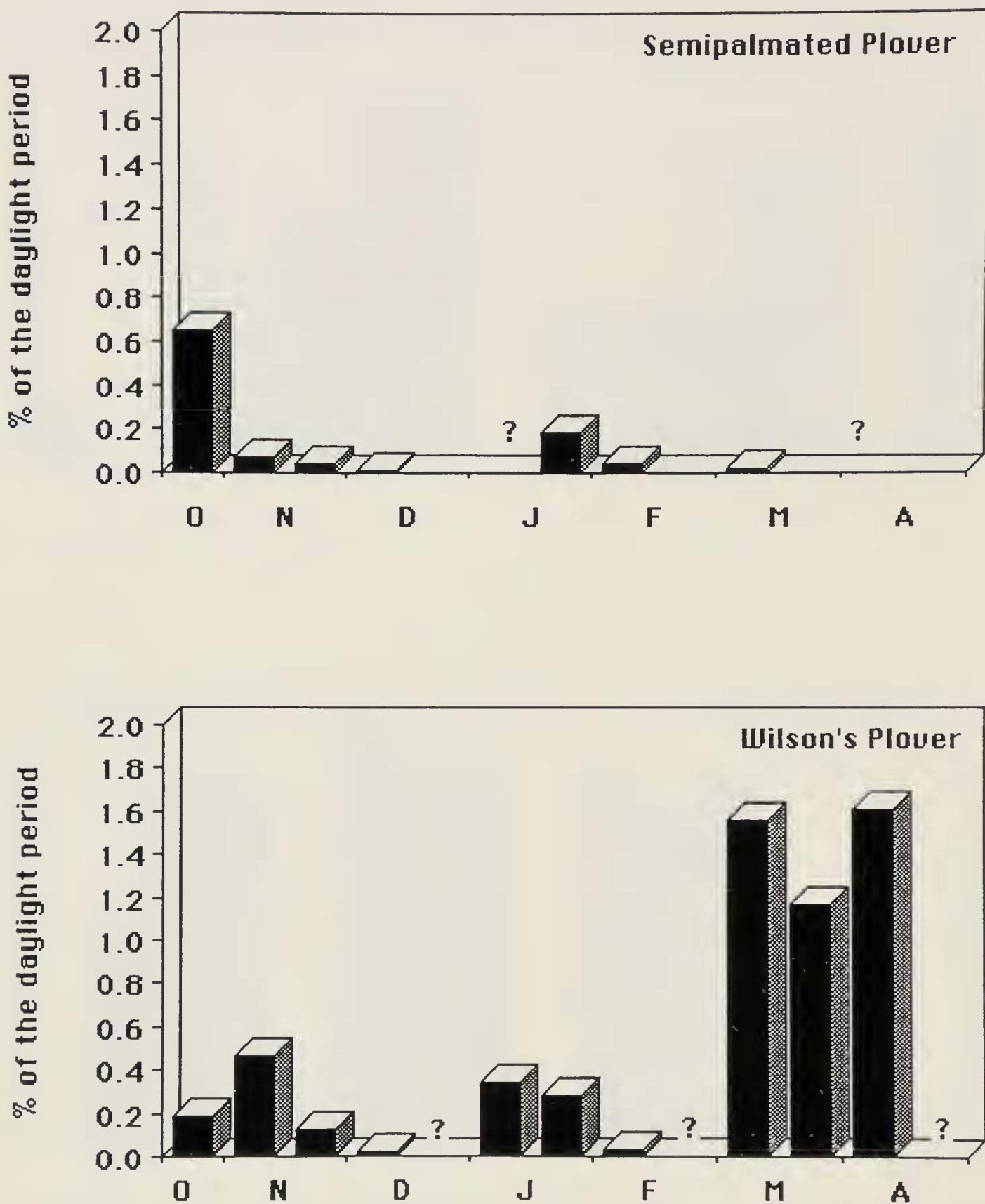


FIG. 3. Seasonal variations in the relative importance of time devoted to aggressiveness during the daylight period. Interrogation marks (?) indicate the absence of data.

The proportion of time spent walking, running, or flying for reasons other than foraging, aggression, or alert was generally low for both species (average = $1.4\% \pm 0.3$ and $1.1\% \pm 0.5$ for Semipalmated and Wilson's plovers, respectively; see Fig. 4). Locomotion in Wilson's Plovers was significantly greater at the end of November and January than in other

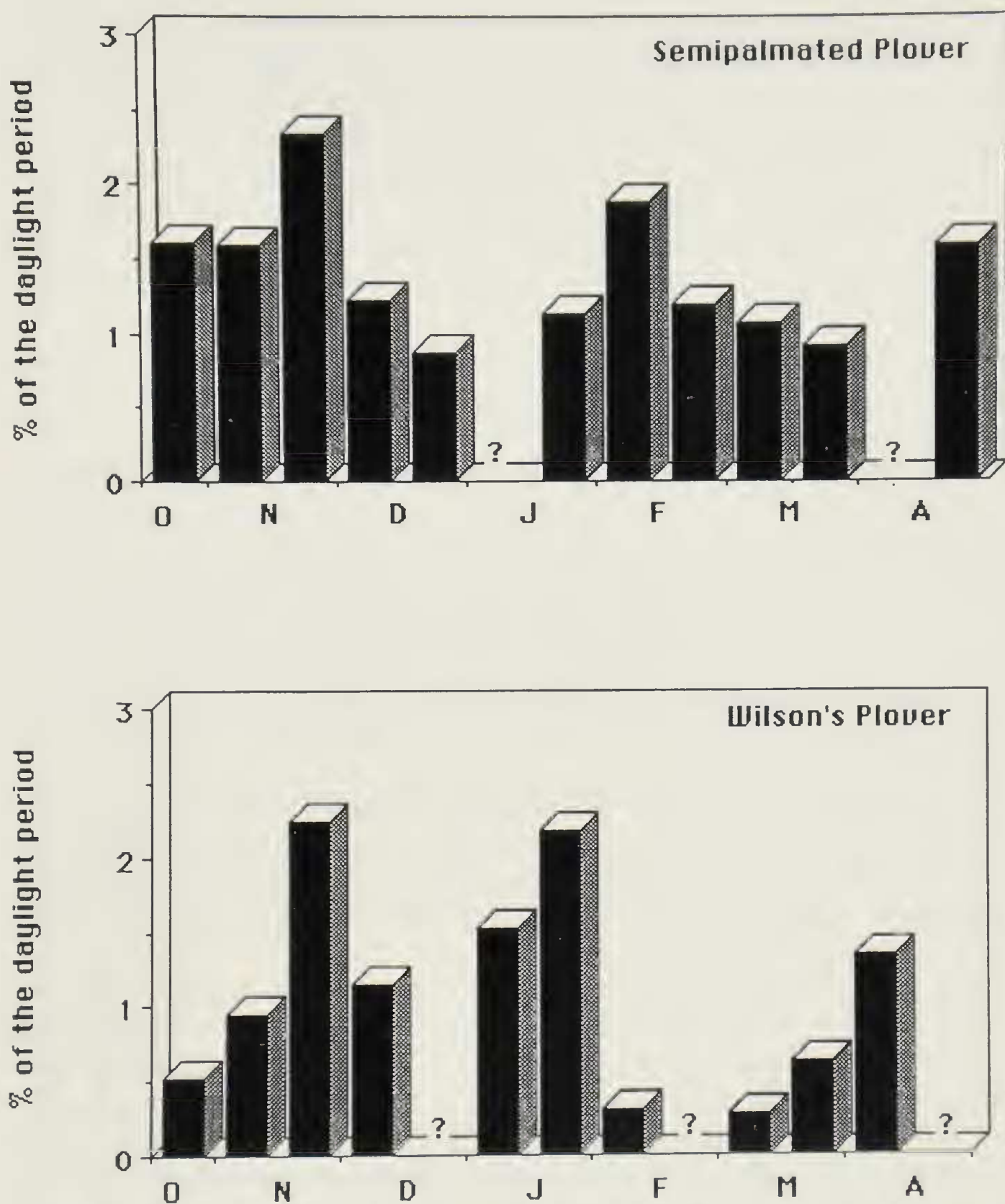


FIG. 4. Seasonal variations in the relative importance of time devoted to locomotion during the daylight period. Interrogation marks (?) indicate the absence of data.

months ($F = 2.17$, $P < 0.05$) but was fairly constant throughout the study period in the other species.

Semipalmated Plovers were alert more often (2.4–7.8%) than Wilson's Plovers (0.9 to 2.8%; $t = 6.64$, $P < 0.001$). However, neither of them showed any significant seasonal variation in alertness.

Daily energy budget of Wilson's Plovers. — Wilson's Plovers principally

ate crabs whose carapace width was equal to a quarter (41.5% of total eaten crabs) or a half (38.6%) of their bill length (Table 4). The estimated number of crabs eaten during the entire daylight period (Table 4) was larger in October, at the beginning of November, and in April (90.1–133.2) than from the end of November to March (1.7–37.3). Their energy content, corrected for CaCO_3 , averaged 11.37 ± 1.34 J/mg of their dry mass ($N = 17$). The relationship between the dry mass (W in mg) of crabs and carapace width (C in mm) is: $\text{Log } W = 3.804 \text{ Log } C - 4.98$ ($r^2 = 0.969$; $N = 207$).

The average assimilatable energy in crabs with carapace width equivalent to a quarter, half, and three quarters the bill length was 38.7, 541.4, and 2531.2 J, respectively.

The mean monthly weight of Wilson's Plovers captured in Chacopata Lagoon was constant during the study period, increasing only slightly (insignificant) in April. Similarly, the DEE ranged from 42.6–45.4 kJ between November and March and was only slightly higher at the end of October and at the beginning of April (Fig. 5, Table 5). During daylight, most of the energy was expended while resting, except at the end of October and the beginning of April when more energy was expended in feeding activities (Table 5). Other activity categories resulted in little energy expenditure.

The daylight energy intake of Wilson's Plovers (Table 6, Fig. 5) decreased sharply between the end of October (99.1 kJ) and the beginning of November and even further toward January (2.4 kJ) and the beginning of February (0.04 kJ). Energy intake increased appreciably only at the beginning of April (86.7 kJ).

The daily energy budget (i.e., daily energy intake minus daily energy expenditure) of Wilson's Plovers consequently showed a large deficit from the end of November to the beginning of April (Fig. 5). The balance was positive only at the end of October, at the beginning of November, and at the beginning of April. It must be noted that the energy intake at the beginning of November, large enough to balance the budget, was not due to greater feeding activity (the latter was just about equivalent to that observed at the end of November, beginning of December and March; see Fig. 3) but to greater foraging success (Table 4).

DISCUSSION

Daylight activities of Semipalmated and Wilson's plovers.—Three activity categories attract special attention, i.e., feeding, resting, and agonistic manifestations for which the seasonal patterns of both species greatly differ. In fact, our results largely confirm the predictions concerning the seasonal variations in the proportion of time devoted to energy intake by

TABLE 4
TIME SPENT FORAGING AND NUMBER AND SIZE OF CRABS CAPTURED BY WILSON'S PLOVERS DURING EACH SAMPLING PERIOD

Sampling sessions	T _f ^b (min)	R _f ^c	Carapace width of crabs ^a						Actual total number of captured prey during ob- servations	Estimated total number of captured prey during the daylight period			
			1/4			1/2					3/4		
			NP ^d	ENP ^e	% ^f	NP	ENP	%			NP	ENP	%
18-21 October	391.7	0.34	30	54.7	41.1	28	51.1	38.4	15	27.4	20.5	73	133.2
11-12 November	74.5	1.21	17	37.4	41.5	16	35.2	39.0	8	17.6	19.5	41	90.1
21-22 November	106.8	0.19	4	7.4	36.4	4	7.4	36.4	3	5.5	27.3	11	20.3
1 December	69.9	0.27	5	10.5	55.6	3	6.3	33.3	1	2.1	11.1	9	18.9
14-16 January	46.6	0.50	5	9.7	41.7	4	7.8	33.3	3	5.8	25.0	12	23.3
29-30 January	49.1	0.13	1	2.1	33.3	2	4.3	66.7	0	0.0	0.0	3	6.4
15-17 February	13.3	0.13	1	1.7	100.0	0	0.0	0.0	0	0.0	0.0	1	1.7
8-9 March	79.4	0.47	8	15.7	42.1	9	17.7	47.4	2	3.9	10.5	19	37.3
22-24 March	78.8	0.33	7	10.7	41.2	6	9.2	35.3	4	6.1	23.5	17	26.0
11-13 April	315.6	0.36	36	46.0	40.4	34	43.4	38.2	19	24.3	21.3	89	113.6

^a Carapace width equal to 1/4, 1/2, and 3/4 plovers' bill length (average bill length of plovers = 20.5 mm; N = 141).

^b T_f = total time of daylight spent foraging.

^c R_f = mean rate of foraging (mean number of prey taken/min).

^d NP = actual number of prey of that type captured during observations.

^e ENP = estimated number of prey of that type captured during the complete daylight period.

^f % = estimated percent of that prey type in the diet.

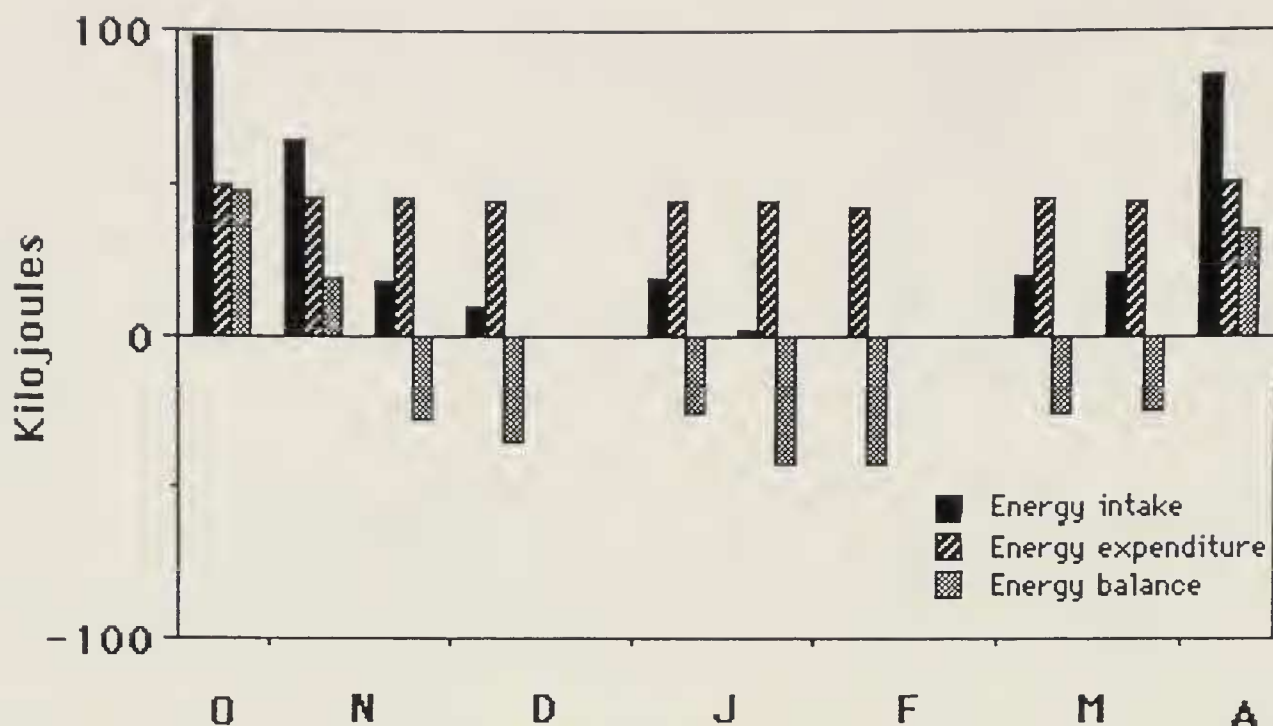


FIG. 5. Seasonal variations in the daily energy budget, on a 24-h basis, of Wilson's Plovers.

migratory and permanent resident shorebirds in the tropics. In addition, in both species, the seasonal resting pattern is typically the reverse of that feeding.

Semipalmated Plovers are present in the lagoons of northeastern Venezuela, including those of Chacopata (Limoges 1987) and Cumaná (McNeil 1970b), especially during fall migration, and between January and April (Limoges 1987). The increase in numbers observed in January suggests regional movements. Semipalmated Plovers undergo their pre-basic molt from August to December (F. Mercier, pers. comm.). The seasonal variations in feeding behavior of the species could be tied to their energetic needs. A certain amount of hyperphagia could take place during pre-basic molt, October–December. Fall-arriving Semipalmated Plovers are likely to be very lean and to devote more time to rebuilding their fat and protein reserves. Plovers devoted more time to feeding in December just before regional movements were observed; however, McNeil (1970a) did not measure the lipid content of the species for the corresponding period. The other period when Semipalmated Plovers devoted more time to foraging corresponds to the pre-migratory hyperphagia which results in the depositing of fat for the northward spring migration. McNeil (1970a) has shown that Semipalmated Plovers, in northeastern Venezuela, have a fat index (% of lean dry weight) averaging 110%, in comparison with values between 15% and 40% in other periods of the year. The species spent less time feeding from January to February, the months when wintering Ne-arctic shorebird migrants have the lowest fat index. The differences be-

TABLE 5
DAILY ENERGY EXPENDITURE (kJ), ON A 24-H BASIS, OF WILSON'S PLOVER

Sampling sessions	Energy expenditure associated with									Total energy expenditure	
	Feeding	Preening	Resting	Flight ^a	Walking	Fight	Ground display	Alert ^b	Running ^c		Nocturnal resting
18-21 October	18.38	0.58	8.56	0.34	0.12	0.00	0.00	0.62	0.03	21.18	49.81
11-12 November	3.49	0.29	17.44	1.47	0.18	0.00	0.07	0.75	0.12	21.39	45.20
21-22 November	5.01	0.73	15.89	0.67	0.62	0.00	0.02	1.03	0.03	21.42	45.43
1 December	3.28	0.35	17.53	0.02	0.31	0.00	0.00	0.48	0.01	21.72	43.70
14-16 January	2.18	0.86	17.58	0.56	0.35	0.00	0.00	0.80	0.11	21.65	44.08
29-30 January	2.30	0.77	17.50	0.32	0.57	0.00	0.00	1.05	0.09	21.50	44.10
15-17 February	0.39	0.54	19.60	0.00	0.09	0.00	0.00	0.75	0.01	21.26	42.63
8-9 March	3.72	0.24	17.70	0.79	0.06	0.00	0.00	1.46	0.12	20.96	45.06
22-24 March	3.70	0.64	17.81	0.15	0.17	0.06	0.58	0.75	0.04	20.70	44.61
11-13 April	14.83	0.39	10.83	1.02	0.38	0.21	0.03	1.73	0.32	20.43	50.17

^a Including all flights associated with alert reactions, agonistic manifestations, and locomotion.

^b Including alert reactions associated with aggressiveness, but excluding flight escape.

^c Including running for feeding, or ground pursuit and escape.

TABLE 6
CONTRIBUTION OF EACH CLASS OF CRAB SIZE TO THE ESTIMATED TOTAL ENERGY INTAKE (kJ) OF WILSON’S PLOVER DURING THE COMPLETE DAYLIGHT PERIOD

Sampling sessions	Carapace width of crabs ^a			Estimated total daily energy intake
	¼	½	¾	
18–21 October	2.12	27.66	69.28	99.06
11–12 November	1.45	19.03	44.50	64.98
21–22 November	0.29	4.00	14.02	18.30
1 December	0.41	3.41	5.31	9.12
14–16 January	0.38	4.20	14.73	19.31
29–30 January	0.08	2.31	0.00	2.39
15–17 February	0.04	0.00	0.00	0.04
8–9 March	0.61	9.57	9.94	20.12
22–24 March	0.41	4.97	15.50	20.88
11–13 April	1.78	23.49	61.38	86.65

^a Carapace width equal to ¼, ½ and ¾ plovers’ bill length (average bill length = 20.5 mm; N = 141).

tween the January–February and the March–April periods in the proportion of daytime devoted to feeding activities by Semipalmated Plovers are similar to those reported by Zwarts (1990) and Zwarts et al. (1990) for several Palearctic shorebird species wintering in Mauritania.

From November to April, Wilson’s Plover devoted much more time to resting than to feeding compared with Semipalmated Plovers. In October (Fig. 1), and also in August and September (B. Gagnon, pers. comm.), the time spent feeding was more than that observed outside the breeding period. The proportion of the day devoted to feeding seemed to vary seasonally with energetic needs. The latter are likely to be higher during the breeding season, which starts in April (McNeil 1970b; B. Limoges, pers. comm.), and during the pre-alternate molt which ends in March–April (F. Mercier, pers. comm.). McNeil (1970b) has shown that Wilson’s Plovers of northeastern Venezuela accumulate fat reserves around March–April which average 37% (reaching 54% and 70%) of the lean dry weight. The fat indices of this resident species are by far lower than those observed during the pre-migratory period of Nearctic migrants (e.g., Semipalmated Plovers; see above and McNeil 1970a) but are sufficient to explain the observed increase of time devoted to feeding in March and especially in April.

In Semipalmated Plovers, aggressiveness may occur in migratory stopovers and wintering quarters (Recher and Recher 1969, Doyon and McNeil 1978, Myers et al. 1979, Myers and McCaffery 1984, Myers 1984). However, the species in general showed little aggressiveness during its stay at

Chacopata (Fig. 3). We observed at least two birds defending a feeding territory at Chacopata indicating that such behavior may take place during migrations. This is in accordance with the findings of Recher and Recher (1969), Myers et al. (1979), Myers and McCaffery (1984), and Myers (1984) in a variety of shorebird species including the Semipalmated Plover. Except in March and April, the time devoted to aggressiveness by Wilson's Plovers also was very short. The increase in aggressiveness observed in March and April is correlated with pair formation and breeding territory establishment (Tomkins 1944; Bergstrom 1981, 1988a, b). Strauch and Abele (1979) also concluded that interspecific competition is not very important between Wilson's, Semipalmated, and Collared (*C. collaris*) plovers.

Semipalmated Plovers devoted more time in alert reactions than did Wilson's Plovers, probably because they spent proportionately more time feeding. Wilson's Plovers, motionless and resting during a large part of the daylight period, were well-concealed and thus showed alert reactions less frequently. In contrast, Semipalmated Plovers, devoting proportionately more time to foraging, had to remain more vigilant of predators. In Chacopata, facing a danger from an aerial predator or during alert reactions for unknown reasons, both species adopted very different strategies; Wilson's Plovers crouched or flattened themselves on the ground, while Semipalmated Plovers flew in compact flocks together with small peep sandpipers (*Calidris* spp.).

Daily energy budget of Wilson's Plovers.—The fact that Wilson's Plovers, compared with Semipalmated Plovers, devoted little time to feeding during daylight raises an important question: Can Wilson's Plovers balance their daily energetic needs with so little time passed foraging and so few prey ingested during daylight or do they need to adopt another strategy to fulfill their energetic requirements? Our results do indicate, in fact, that daytime foraging is insufficient, at least from November to April.

In many species of shorebirds of northern regions, daytime foraging seems insufficient for the birds to fulfill their energetic needs during the winter (see Pienkowski et al. 1984). For example, in Britain during mid-winter, daylight foraging in Northern Lapwings (*Vanellus vanellus*) provides less than 10% of the birds' existence energy requirements (McLennan 1979). The same may occur in tropical environment (Engelmoer et al. 1984). Insufficiency in daytime energy intake was reported for Bartailed Godwits (*Limosa lapponica*) in Mauritania (Engelmoer et al. 1984) and juvenile Curlew Sandpipers oversummering during the boreal summer in South Africa (Puttick 1980). In tropical environments, high daytime temperature and desiccation of the substrate surface may cause prey to come to the surface less frequently (Burger 1984, Batty 1991) and are

likely to be responsible for such a deficit. However, the body mass of Wilson's Plovers at Chacopata did not decrease between the end of November and the beginning of April, even though diurnal foraging appeared insufficient to fulfill their daily energetic requirements. The energy deficit measured in Wilson's Plovers during that period was only apparent.

Two strategies could compensate for a diurnal deficit: the use of accumulated reserves, principally fat, and/or nocturnal feeding.

Many shorebirds wintering in boreal regions accumulate fat reserves to sustain their energetic demands during winter months (Evans and Smith 1975, Davidson 1981, Dugan et al. 1981). A similar phenomenon has also been reported for birds that reside permanently in the tropics, such as Black-necked Stilts which accumulate such reserves "in preparation for the dry season, when food may be relatively scarce for this species" (McNeil 1971). The diurnal energetic deficit observed in Wilson's Plovers is apparently not compensated for by accumulated fat since body mass did not vary seasonally. In addition, Wilson's Plovers collected in other sites close to Chacopata on the northeastern coast of Venezuela maintained, the year round, a very low fat content (18.5–24.7% of the lean dry weight), except just before breeding.

It was shown recently that Wilson's Plovers, as well as Semipalmated Plovers, are active and forage during nighttime at the site of the present study, especially during low tides (McNeil and Robert 1988; Robert and McNeil 1989; Robert et al. 1989; B. Gagnon, pers. comm.). In the daytime, they concentrate their feeding activities during periods of low tide (Strauch and Abele 1979), but do not feed during the totality of these periods in spite of the fact that they do not eat enough to balance their needs. This study shows, however, that they devote proportionately less time to feeding during daylight hours than Semipalmated Plovers and suggests that, at least from November to March, they forage mainly during the night. The time devoted to foraging by Wilson's Plovers during the day was also greatly reduced, in comparison with that of other shorebird species wintering in Arctic (see Puttick 1984), northern temperate (Maron and Myers 1985), southern temperate (Puttick 1979, Hockey 1984), and tropical (Engelmoer et al. 1984, this study) regions.

It thus appears that Wilson's Plovers have a balanced daily energy budget, the birds counterbalancing a diurnal energy deficit by a nocturnal energy intake. However, what are the reasons for a mainly nocturnal foraging strategy?

There are two broad hypotheses, the "preference hypothesis" and the "supplementary hypothesis." The former is that this strategy provides the more profitable or the safer, feeding opportunities; the other is that night feeding occurs only when daytime feeding has been inadequate to meet

the birds' requirements (McNeil, in press). The following arguments give greater support to the "preference hypothesis."

In tropical environments, a decrease in daytime prey availability may result from high temperatures and desiccation of the substratum surface (Burger 1984, Batty 1991). Prey activity, and their availability, may be greater during the night than during daylight (Dugan 1981; Pienkowski 1983a, b; Townshend et al. 1984). Robert et al. (1989) observed this in February at one of the Chacopata foraging sites for many prey types. Their study did not include crabs. In spite of the lack of data comparing diurnal and nocturnal availability and/or accessibility of *Uca* crabs, the preferred prey of Wilson's Plovers, we believe that their nocturnal activity is not due to a daylight food shortage. The Chacopata mudflats are swarming with millions of small crabs, both in the day and at night.

On the other hand, special techniques or strategies could be needed to catch *Uca* crabs: not only do they live in deep burrows out of reach of plovers' bills, but when on the surface, they flee as soon as a bird comes within several meters. According to Zwarts (1985), there is a circle with a radius of 1–3 m around a feeding bird where there are no *Uca tangeri* on the surface (see also Summers 1980). Plovers, by making quick dashes, are able to catch fiddler crabs, but they often pause and wait for the circle devoid of crabs to become smaller as *Uca* reappear on the surface. It is possible that the radius without crabs on the surface around a feeding Wilson's Plover could be smaller during darkness than during daylight. In addition, Zwarts (1990) found that no *Uca* were present at the surface of mudflats when low water occurred in the second half of the night or in the early morning (02:00–08:00 h). At night, the crabs also fed closer to their burrows than during the day (Zwarts 1990). According to Zwarts and Dirksen (1990), *Uca* are very easy to catch in such a situation. Consequently, in the case that *U. thayeri* behave as *U. tangeri*, it would be easy for Wilson's Plovers and other shorebirds to catch them by a wait technique during the first part of the night.

Wilson's Plovers seem better adapted for night feeding than Semipalmated Plovers. Their bill, longer and stronger, is well fitted to catch highly mobile crabs (measuring on the average 7.82 mm) at the surface of the substratum (Strauch and Abele 1979). Semipalmated Plovers are generalist or opportunistic feeders, and have a small bill allowing them to catch varied but smaller prey measuring, on average, 1.81 mm (Strauch and Abele 1979). On intertidal mudflats, their diet largely comprises small polychaeta, buried in the substratum, small insects, crustacea and mollusca (Strauch and Abele 1979, pers. obs.). All these prey types are likely to be less conspicuous at night than the crabs taken by Wilson's Plovers.

The period of low daylight foraging activity of Wilson's Plovers, ex-

cepting April, roughly corresponds to the months when Peregrine Falcons (*Falco peregrinus*) are present over the Chacopata lagoon complex. The latter arrive in November and leave at the end of April (Limoges 1987). The presence of falcons in the lagoon complex could result in some shorebird species not congregating in some areas (e.g., small expanse surrounded by mangroves) during daylight because of possible predation, in spite of their richness in prey organisms. Rather, the shorebirds would exploit them only during darkness (Robert et al. 1989). Limoges (1987) also observed that many of the smaller shorebirds congregate in significantly higher numbers when Peregrine Falcons start chasing them over the Chacopata lagoon. Such a behavior could reduce individual risks of being captured by the aerial predators (Vines 1971, Page and Whitacre 1975). As far as Wilson's Plovers are concerned, gregariousness increased, but not significantly, when the falcons appeared (Limoges 1987). However, compared to Semipalmated Plovers, Wilson's Plovers foraging is dispersed and solitary. According to Limoges (1987), they are more gregarious when roosting than when foraging. Wilson's Plovers could gain more by roosting during daytime, instead of foraging. Being less active, more gregarious, and more concealed, they would be less exposed to predation from Peregrine Falcons or other aerial predators.

Finally, the basal metabolic rate tends to be lower in birds from the tropics compared to birds from colder regions; one explanation for this is that reduced endogenous heat production in the tropics may be advantageous in avoiding heat stress. Since metabolic rates in shorebirds are higher than in other families of birds (Kersten and Piersma 1987), the Chacopata shorebirds may be especially susceptible to warm circumstances. However, our suggestion is that this could apply equally to both species of plovers. There are no data with which to examine whether or not they suffer heat stress, but both species seem to behave differently under the midday sun. On many occasions, Semipalmated Plovers left the mudflats to get shade under mangroves. In contrast, Wilson's Plovers rested in small depressions on the mudflats, apparently seeking protection against midday and afternoon strong winds rather than against full sun (A. Morrier, pers. obs.).

Limits of the method for the daily energy budget. — Kersten and Piersma (1987) present an equation for predicting the basal metabolic rate of shorebirds, derived from data on northern species. Of the several equations used for estimating the basal metabolism of non-passerine birds (see Kendeigh et al. 1977), the equation of Aschoff and Pohl (1970) gives the lowest values, over-estimating the basal metabolism of many tropical species, and under-estimating by 42% that of many shorebirds (see Kersten and Piersma 1987, Mathiu 1989). However, since the present study took place in a tropical environment, the model of Aschoff and Pohl

(1970) is more conservative and likely to be more adequate for Chacopata Wilson's Plovers.

The values for the K-factors allocated to each activity category in calculating the energy expenditure (Table 3) do not result from studies on Wilson's Plovers. Such data are lacking for shorebirds. In the present study, feeding activity, diurnal resting, and the presumed nocturnal resting represent from 92.0 to 97.4% of the total energy expenditure. Other values for the K-factor were used for shorebirds, such as 5.8 (Puttick 1980) and 3.0 (Brunton 1988, Maxson and Oring 1980) for feeding. As did Brunton (1988) and Maxson and Oring (1980), we used a K-factor equal to 1.24 both for diurnal and nocturnal rest. Puttick (1980) used a K-factor equal to 1.35 for diurnal rest.

Our values for energy expenditure thus seem under-estimated for many reasons. First, as mentioned above, it has been shown that Wilson's Plovers are active and feed during nighttime at the site of the present study. Nocturnal activities are particularly important from November to March. The cost of such activities was not included in our estimates, because we presupposed that Wilson's Plovers were resting from dusk to dawn. In addition, Wilson's Plovers suffer their pre-alternate molt from February to April (McNeil 1970b; F. Mercier, pers. comm.). Pre-basic molt takes place in August and September (F. Mercier, pers. comm.), but may extend up to December (McNeil 1970b). The energetic cost of molting and thermoregulation also were not considered here.

The actual energy intake, on the other hand, is likely to have been over-estimated. In the present study, except during mid-winter, crabs whose carapace width was equal to three quarters of the length of the plovers's bills counted for 10–20% of their diet and for 49–76% of their total energy intake. The relationship between the energy content of crabs and their size is exponential, and a slight over-estimation of the latter would suffice to over-estimate energy intake appreciably. In Panama, Wilson's Plovers were found to have about the same diet (96% crustacea) as at Chacopata, but the maximal width of ingested crabs was equal to 10 mm. Crabs equal in size to three-quarters the bill length of plovers are likely too big to be swallowed. It is quite possible that we sometimes over-estimated the size of crabs, especially because of the difficulty in visualizing the carapace without including the legs.

ACKNOWLEDGMENTS

This study was supported by the Natural Sciences and Engineering Research Council of Canada, Fonds F.C.A.R. (Gouvernement du Québec), and the Univ. de Montréal. We thank F. Mercier for help during the field work and access to part of her unpublished data, D. Boisclair, L. Carpineta, and P. Drapeau for helpful comments on the manuscript, P. Jolicœur

for advice in data analysis, M. Anctil, P.-P. Harper, and B. Pinel-Alloul for access to part of their research equipment. We are also indebted to colleagues of the Universidad de Oriente, and in particular, J. Rodríguez S. co-responsible with McNeil for the collaboration agreement between that university in Venezuela and the Université de Montréal, as well as M. T. Díaz.

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